THE SOUTH AMERICAN DISTRIBUTION OF THE MEMECYLEAE (MELASTOMATACEAE) IN RELATION TO THE GUIANA AREA AND TO THE QUESTION OF FOREST REFUGES IN AMAZONIA

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ABSTRACT

Distribution patterns in the tribe Memecyleae show only one major center of differentiation in or immediately adjacent to Amazonia, in the northeastern Guianas and nearby Amapá. Six examples in Mouriri involving eight species illustrate different degrees of differentiation related to this region. Three of the examples are clinal, all with the most specialized members of the cline occurring in or near the Guianas. It seems possible to account for all but one of these distributions largely on the basis of present conditions, although with some difficulty; the explanation of the exceptional case appears to require moister conditions in the past and that of the others is facilitated by theorizing slightly drier conditions of the near past and moister conditions at some other time. The moister conditions may have been related to the proposed interglacial ocean embayment of the Amazon Valley. Habitat preferences and tolerance ranges are probably factors. Distribution patterns do not provide strong evidence for proposed past forest refuges in the rest of Amazonia. The patterns strongly reflect sharp differences in present conditions such as those at the more or less isolated relatively moist forests of north coastal Venezuela, coastal Colombia, and coastal southeast Brazil, as well as the coastal Guianas, but not lesser differences like the rainfall maxima of west and southwest Amazonia.

The tribe Memecyleae of the Melastomataceae is a group of tropical trees, rarely low and shrubby, which includes the two genera Mouriri Aublet, with 75 species, and Votomita Aublet, with six (Morley, in press). In South America the tribe ranges from Colombia south to Bolivia on the west and to Santa Catarina, Brazil, on the east, covering much of the northern 3/5 of the continent. Specific and subspecific differentiation across the area can be shown in some instances to be related to existing climatic zones, certain of which correspond to forest refuges postulated for tropical South America by Haffer (1969, 1974), Vanzolini (1970), Vanzolini and Williams (1970), Prance (1973), and others.

The distribution pattern most often repeated and presenting the most striking examples of subspecific differentiation is one in which plants of the Guianas differ from their relatives to the west and south. More specifically the area concerned includes north Surinam, northeast French Guiana, and nearby parts of Amapá of Brazil, where the annual rainfall is 2000-3000 mm or more. Westward from here the rainfall drops to 1500 mm or less in a relatively dry region, then increases again to 2000 mm and more. Six different examples in Mouriri involving eight species illustrate differentiation related to these regions, and tell us that the latter have been a major factor in the recent evolution of these groups.

Different degrees of divergence have occurred in the different examples. Specific differentiation is exemplified by two pairs of closely related species (fig. 1): (1) M. crassifolia Sagot of north Surinam, northeast French Guiana, and Amapá and northeast Pará of Brazil, and M. ficoides Morley of the Manaus area in Amazonas, Brazil and in south Amazonas, Venezuela; and (2) M. dumetosa Cogniaux of northeast French Guiana and nearby Amapá, east Pará, and northwest Maranhão in Brazil, and M. densifoliata Ducke of the northeast quarter of Amazonas, Brazil, adjacent Pará, and central Roraima. Both pairs have similar distributions, and interestingly enough both belong to the same well-defined section of Mouriri, Cyrtotheca.

The two regions occupied correspond very roughly to two of the forest refuges postulated by Prance, the Manaus and the Guiana, but extend far out of them and in fact scarcely enter the Guiana refuge as shown. The southeast parts of the ranges of M. crassifolia and M. dumetosa, from Amapá into northeast Pará and northwest Maranhão, do not coincide with the center of differentiation strongly suggested by the following examples; if there was an ocean embayment up the Amazon Valley during the interglacials as has been proposed then it is probable that these species were restricted to the northwest during the latest inundation and migrated southeastward later.

In the first pair of species, M. crassifolia and M. ficoides, divergence into well-defined species has occurred. Mouriri dumetosa and M. densifoliata are not so well distinguished but have been retained as species in the absence of more definitive information on their relations. Mouriri densifoliata has a somewhat broader known distribution than M. ficoides, the corresponding member of the other pair, and moves east of the 2000 mm line on the Amazon, but seems essentially like the latter species in distribution. It seems likely, therefore, that climatic isolation has been largely responsible for the divergence of the members of these pairs, whether isolated under present conditions or modified ones of the past.

Differentiation within a species into two slightly variant but widely separated populations is found in M. oligantha Pilger, which occurs in western Amazonia and in Amapá and French Guiana (fig. 2). Despite the great gap in distribution, known differences between plants from the two regions are very small. At present the only differences I find are in anther size and shape. Anthers from the east are 2.4-3.7 mm long, while those from the west are 3.1-4.4 mm long, with slight accompanying differences in form and position of parts, by themselves insufficient evidence for the recognition of two taxa. The possibility remains that further collecting will decrease or fill the gap, or that differences will be found in the fruits or seeds. Mature fruits are known only from Amapá at present. If the two populations should later prove to be separate species, they will almost certainly be a very closely related pair.

Clinal gradation between the Guiana area and territories to to the west and south is found in three widespread species, M. grandiflora, M. vernicosa, and M. guianensis; these will be discussed in turn. Mouriri grandiflora DC. (fig. 3) is found from the upper Orinoco drainage in Colombia and Venezuela through the three Guianas where it is common, through the western Amazon drainage down to Bolivia, and in Amazonas, the northern 2/3 of Pará, the north tip of Goiás, and Amapá of Brazil. In this species, stomatal crypts are the primary clinal character involved. The crypts are most often present in the east and northeast parts of the range, and are almost completely lacking along the western periphery; a gradient appears to be present from one region to the other, although with a relatively sharp break between Para and Amazonas in Brazil. Pieces of leaves of 46 collections were cleared, stained, and mounted for microscopic examination, while leaves of 41 more were examined under high magnification without clearing and staining; the latter method is nearly as reliable as the former. In the three Guianas, crypts were present in all of the 19 collections checked; in nearby Amapá, Brazil, five of the collections examined had crypts, six did not. In Pará, 21 collections showed crypts and three did not. A single collection from extreme northern Goiás had crypts. In Amazonas, on the other hand, five collections showed crypts and nine did not. In Acre and in Bolivia, Peru, Colombia, and Venezuela three specimens were with crypts and twelve without.

In seeking an explanation of this distribution we can compare it with the climatic zonation. The rainfall map of Reinke (1962) as adapted in Haffer (1969) and Prance (1973) shows a broad relatively dry zone across the western half of Pará and extreme eastern Amazonas, grading to the east and west into moister areas, and extending northwest into Venezuela, touching western Guyana. In so far as the dry region sweeps across east of the center of Amazonia, and crypts are most common in the east, there

is a very general conformation with the expectation that crypts
would be developed in drier areas as a mechanism to reduce water
loss. However, a major contradiction exists in the prevalence of
crypts in Surinam and French Guiana, from whence came most of the
Guiana collections, and in Amapá and eastern Pará, all part of a
wet region. It appears as if the crypts had originally developed
in the dry zone and spread, through introgression, into adjacent
moister areas; expansion and contraction of the dry area with
climatic change (Haffer, loc. cit.) may have played a part. The
similarity of this distribution pattern to the two following
clines, which focus on French Guiana, is suggestive, but the two
situations do not seem to be quite the same, although some of the
same factors may be involved. The occurrence of two dry seasons
in much of the Guianas could be a factor; however, the total
rainfall of most of the area is relatively high. A more complete
study with a more detailed rainfall map is needed.

     A papillose under surface of the leaf also correlates with
distribution in this species, but in this case the character is
only western. Six collections exhibit a papillose surface, and
these come from Amazonas in Colombia, Loreto in Peru, and western
Amazonas in Brazil. The functional significance of this surface
if any is unknown.

     Mouriri vernicosa Naudin (fig. 4) is not as widespread as
the preceding species, ranging from the upper-middle Orinoco
south to Vaupés in Colombia and to the Amazon in Amazonas, Bra-
zil, and east to the Guianas and northwest Maranhão and up the
Tocantins to 6⁰ S. The clinal variant here is the form of the
fruit, specifically the ribbing of its outer wall. In French
Guiana the fruits have nine or ten very prominent ribs extending
the whole length of the fruit, a form which can only be regarded
as highly modified. Away from that country, however, the ribs
tend to be less prominent, are often fewer, and may extend only
part of the way toward the apex from the base, being scarcely
noticeable in some cases. The limited information presently
available suggests that the situation is clinal, with the ribb-
ing becoming less pronounced as one goes farther from French
Guiana.

     In a collection from the Rio Xingu, for example, ca. 770 km
from Cayenne, the ribs are small and narrow; five or six of them
reach the apex but the others become indistinct ca. 3/4 of the
way up. In another plant from the Rio Tocantins ca. 1050 km
from Cayenne, the fruits which were unfortunately immature
showed ridges only on the lower 1/3 of the fruit. The immature
fruits of still another collection from Venezuela ca. 1650 km
from Cayenne had indistinct ridges, apparently present on the
lower 1/3. In another plant from the upper Rio Negro of Brazil
ca. 1700 km from Cayenne, only three ridges can be found on the

fruit, low and narrow, running ca. 3/4 of the way to the apex.
And the fruits of a collection from Amazonas in Colombia, ca.
2000 km from Cayenne, have ten very low ridges visible 3/4 of the
way to the apex. Immature fruits from French Guiana show ridges
as distinct as on the ripe fruit, therefore the ridging of other
immature fruits should be at least somewhat indicative of the
form of the mature fruit. The French Guiana fruits are so dis-
tinctive that one wonders if those plants may represent a separ-
ate taxon; however, floral characters do not suggest it, and
fruiting collections are too few to be sure.

Mouriri guianensis Aublet (fig. 5) is most widespread of
all, ranging from Trinidad up the Orinoco and south in Brazil
through the east half of Amazonas as far as the region of Corumbá
in Mato Grosso, and south through the three Guianas and the cen-
tral and eastern states of Brazil to Rio de Janeiro. In this
species a pattern similar to that of M. vernicosa is found but
involving in this instance leaf and flower characters. The
leaves are typically ovate to ovate-elliptic and with the lateral
veins raised and moderately visible when dry. The ovate forms,
however, are largely restricted to coastal or near-coastal reg-
ions such as Trinidad, Guyana, Surinam, French Guiana, and Pará,
Ceará, Bahia, and Rio de Janeiro of Brazil (ovate-elliptic forms
also occur in these areas). In these regions the lateral veins
are usually quite conspicuous when dry. At the other extreme,
elliptic forms occur occasionally in west-central Pará, Amazonas,
Mato Grosso, and Piaui, and the lateral nerves in these leaves as
well as in ovate-elliptic leaves of the same regions tend to be
flat and nearly invisible when dry. Nearly invisible lateral
nerves have also been seen from Maranhão and Bahia. The petiole,
another leaf variable, is usually 1.5-3.5 mm long but in west-
central Pará, central Amazonas, and Mato Grosso it may be up to
4.5 or occasionally 5.0 mm long.

Of all the variables in this species, the most instructive
is that of ovary size, as an indication of locule and ovule num-
ber. The locules and ovules vary respectively from 2-5 and 9-33,
and the differences are reflected rather accurately in the out-
side diameter of the ovary. This convenient parameter, when
measured on dried material, varies from 1.0-2.2 mm. The smallest
ovaries, and therefore the most reduced and specialized, occur in
the Guianas, and larger sizes are found as one goes farther away
from this center, especially toward the interior. The pattern
resembles that of leaf form and venation and petiole length but
is more precise. The differences in size appear to be generally
clinal in nature, although great diversity is found in some reg-
ions; if sharp breaks exist, I have not found them. French
Guiana appears to be near the center of size reduction.

Specifically, sizes are as follows: French Guiana, 1.0-1.2 mm (8 collections); Surinam, 1.2-1.3 (2 colls.); Guyana, 1.0-1.8 (3 colls.); Venezuela, 1.2-1.9 (4 colls.); Trinidad, 1.2 (1 coll.); in Brazil, Amapá, 1.0-1.2 (1 coll.), Maranhão, 1.3-1.7 (4 colls.), Piaui, 1.3-1.6 (3 colls.), Ceará, 1.3-1.8 (3 colls.), Bahia, 1.4-1.6 (3 colls.), Minas Gerais, 1.6 (2 colls.), Rio de Janeiro, ca. 1.4 (1 coll.), interior Pará, 1.5-2.0 (6 colls.), Amazonas, 1.2 (Rio Branco)-2.2 (3 colls.), Mato Grosso, 1.5-2.0 (6 colls.).

In the case of M. grandiflora the primary variable character, presence or absence of stomatal crypts, has as noted an obvious adaptational value. The region of the crypts' greatest concentration may be in the dry zone just west of the Guianas, and therefore this cline may not be exactly comparable with the other two. The variables in the other two species, fruit form, leaf shape, and ovary size, are not plainly adaptational; in both cases French Guiana near the coast and probably nearby parts of Amapá, Brazil seem to be the center of the most extreme forms. It may be relevant that the distribution of the endemic species M. francavillana Cogniaux in these countries appears to approximate what I judge to be the core of the area of specialization. Therefore in all three clines the less specialized forms occur in the broad regions away from the Guianas while the most specialized ones are concentrated in or near the Guianas, a Guiana focus.

In all six examples the coincidence of distribution patterns is close at least at the Guiana end and is strong evidence of a fundamental basis for all. Prance (1973) has sought further for such coincidences, looking particularly for areas of repeated endemism, and on the basis of these has proposed sixteen forest refuges, eight of them in Amazonia proper. If we examine the Memecyleae on this basis we can identify about 30 species of the South American rain forest that can be said to have distributions sufficiently localized to be possible indicators of points of origin. Among these we find an inconsistent fit with the proposed refuges. Mouriri pseudo-geminata Pittier fits the northern Venezuela refuges of Vanzolini, Haffer, and Prance and occurs also in Trinidad, while M. rhizophoraefolia (DC.) Triana is found in Prance's Imataca refuge as well as in and between the north coastal refuges of Venezuela and in Trinidad and Tobago (these two species are probably not of the true rain forest); M. micranthera Morley and M. pachyphylla Burret fit the Chocó refuge of Haffer and Prance, and M. angustifolia Spruce ex Triana and M. spruceana Morley are close to but not within the Imerí refuge of both authors; M. duckeanoides Morley fits the Manaus refuge of Prance and M. densifoliata Ducke and M. froesii Morley are close to it; V. plerocarpa (Morley) Morley is close to the Olivença refuge of Prance; V. monadelpha (Ducke) Morley falls within the

Belém refuge of both Haffer and Prance, and a closely related but
unidentified specimen (Stahel 293) comes from the inland Guiana
refuge; V. orbinaxia Morley fits the Belém refuge of Haffer but
not of Prance; M. obtusiloba Morley is very close to Prance's
Belém refuge but not to that of Haffer; and M. arborea Gardner,
M. doriana Sald. ex Cogn., M. chamissoana Cogn., and probably M.
bahiensis Morley and M. regeliana Cogn. match the Serra do Mar
refuges of Müller (1968), Haffer, and others, simply termed
"coastal forest" by Prance. Mouriri francavillana Cogn. and V.
guianensis Aublet are in the Guianas but are near-coastal, not
well inland where the refuge is supposed to have been. And M.
ambiconvexa Morley, M. barinensis (Morley) Morley, M. dimorphan-
dra Morley, M. eugeniaefolia Spruce ex Tr., M. exadenia Morley,
M. floribunda Markgraf, M. longifolia (HBK) Morley, M. micradenia
Ducke, M. monopora Morley, M. tessmannii Markgraf, and M. unci-
theca Morley and Wurdack, with V. orinocensis Morley, fit none of
the proposed refuges; all are from central to southwestern to
western to northwestern Amazonia except for M. longifolia and V.
orinocensis from southern and west-central Amazonas, Venezuela,
respectively, and M. barinensis from the western Orinoco drainage
in Venezuela. All the preceding species are mapped elsewhere
(Morley, in press).

The foregoing naturally depends on the adequacy of the plant
collecting across the region. In spite of the great efforts of
many dedicated people, these would be the first to admit that
much remains to be done. Many distributions will be expanded and
gaps filled in the future. There still exists at present the
possibility, hopefully remote, that some of the apparent concen-
trations of species as at Manaus and Belém are only areas of more
intensive collecting.

DISCUSSION

The dominating feature of the distribution patterns of the
Memecyleae in Amazonia is the Guiana relation, as the six ex-
amples illustrate. No such consistency over such a wide area in-
volving so many species occurs elsewhere in the tribe. The for-
ces responsible for these parallel cases of differentiation are
not fully clear, but must be related to present or past environ-
mental or geographic differences. First we must ask, can these
cases be accounted for on the basis of the present environment,
without invoking changes of the past? I think it might be poss-
ible with the exception of M. oligantha, but not without certain
difficulties. Breadth of environmental tolerance might have been
a major factor. Those species which can grow with relative free-
dom in the intervening dry zone as well as in the moist areas on
both sides develop few or no differences, while species which can
exist only here and there in the dry belt have restricted gene
flow between the moist zones so that divergence can take place

but without a break in continuity, the result being a cline.
Other species, with narrow tolerances, can grow only in the moist
areas; once the gap from one to the other has been bridged by
long-distance dispersal, differentiation is free to proceed, as
on islands. If this is a valid explanation then one might expect
more speciation to occur in groups with moderate to rather narrow
tolerance ranges than in those with broad tolerances, since
smaller environmental differences would serve as barriers. Such
a phenomenon should be more noticeable in broad regions of rela-
tively slight ecological differences, such as the Amazon basin.
The requirement of long-distance dispersal (to be discussed be-
low) in this and the following theory is a drawback of uncertain
magnitude.

A somewhat different explanation would be that the various
taxa prior to differentiation simply had differing habitat re-
quirements, and that in some cases those habitats occurred with
varying frequency within the dry zone and in others were lacking.
Mouriri grandiflora, M. vernicosa, and M. guianensis all grow
above and below flood level but are often or usually found near
water, which would make it possible for them to exist in the dry
zone along streams but with restricted distributions in the gen-
eral area. The habitat preferences of the other species as giv-
en by the collectors do not reveal clear-cut differences between
them and the preceding three. Although M. crassifolia and M. fi-
coides occur almost entirely in primary forest above flood level,
M. dumetosa grows above flood level but often at the edge of wa-
ter, and M. densifoliata and M. oligantha are found both above
and below flood level. Therefore for the present we must infer
habitat differences from the distributions. Both habitat diff-
erences and tolerance ranges may be involved in these varying de-
grees of differentiation.

Other less obvious parameters of the environment may of
course act as driving forces. The abundance of suitable animal
pollinators may be such a factor, although most Mouriri flowers
do not appear from their structure at least to require very spe-
cific pollinators. Type of fruit eater could be another factor.
Still another might be the occurrence of two dry seasons in much
of the Guiana region.

The thesis of climatic change, as outlined by Haffer, would
appear to provide a ready explanation for these distributions.
Populations become cut off in the Guiana area by climatic change,
they diverge, and then after climatic reversal either remain di-
vergent under present conditions, or if their habitats and toler-
ance ranges permit re-occupation of the drier zone, they may form
a clinal continuum through hybridization, providing their genetic
differentiation has not become too great. To be sure, none of
the six examples cited illustrates a clear-cut case of apparently

"secondary contact", of closely related groups being brought to-
gether again, although one or more of the clines could have had
such an origin. However, all could be explained on the basis of
climatic change, except that the gap between the isolated members
of the pairs of species would have to be accounted for: the gap
between M. densifoliata and M. dumetosa, and between M. ficoides
and M. crassifolia, not to mention the still greater gap between
the two forms of M. oligantha. The smallest gap is of roughly
820 km, between M. densifoliata and M. dumetosa. The existence
of these gaps seems to mean one of two .things: either the clima-
tic reversal is not complete, leaving separated populations still
separate, or these separated populations were produced by long-
distance dispersal and not by climatic change. Both assume that
the habitat requirements of the species have not changed signifi-
cantly from those of the original forms. Since it has been con-
cluded by some (Haffer 1974, p. 142) that the reversal is com-
plete, there appears to be a conflict here if climatic change is
to be invoked. It seems most likely to me that moister condi-
tions did exist in the past which brought the ancestors of the
groups concerned closer together, perhaps completely so.

A third alternative is that the suggested deep ocean embay-
ment of the interglacial periods may have modified the moisture
conditions in its vicinity and permitted an approximation of
currently separated moist zones without an overall climatic
change, or even in opposition to such a change.

Such an embayment with locally moist conditions offers the
most satisfactory solution to the problem presented by M. oligan-
tha. The difficulty here lies in the great size of the gap be-
tween the two populations of this species and the fact that the
plant's large fruits and seeds make long-distance dispersal an
unlikely event. The fruits are up to 32 mm high and 46 mm thick,
and the seeds reach 21 mm high, 23 mm wide, and 12 mm thick.
While generally moister climatic conditions could have brought
together the ancestors of the two populations, such an explana-
tion would require a considerable westerly migration of the west-
ern population, for reasons unknown. The gap would be easily
accounted for, however, if the ancestors had grown along the edge
of the proposed embayment, becoming split into two parts as the
latter withdrew.

If the embayment theory holds then of course the explana-
tions of the other plants discussed here would have to be brought
into agreement with it.

If, however, a gap narrower than the present one did exist
at the initiation of the separation of some or all the groups
concerned, that distance then might have been bridged relatively
easily by long-distance dispersal. Such dispersal overland can-

not be ruled out, with streams, storm winds, and birds, or a com-
bination of the latter two being the most likely carriers.
Transport of edible or otherwise useful fruits by natives is ano-
ther possibility. Fruits in the Memecyleae are berries edible to
animals (some are eaten by humans) and apparently seed dispersal
in most cases is by bird; therefore plants of the tribe are logi-
cal candidates for long-distance dispersal by this means. Long-
distance flights would seem a very probable phenomenon for for-
est birds flying over wide expanses of continuous grassland,
and an unlikely occurrence but still a possibility for such birds
flying over broken or continuous forest.

The same problem of climatic reversal vs. long-distance dis-
persal applies of course to all of the proposed refuges that are
presently isolated. Either the climate was more humid than now
at some time in the past, perhaps before the latest climatic
fluctuations, thereby greatly reducing the isolation of these
areas, or long-distance dispersal must have been involved in
their formation.

In describing the apparent clinal situation in M. vernicosa
it was noted that the distinctness of the fruit form in French
Guiana raised the possibility that plants of that area might
actually be a separate taxon. The same observation also arouses
the suspicion that the isolation of the Guiana pocket may once
have been more complete than it now is, so as to permit such a
pronounced differentiation to develop. The refuge theory would
provide that isolation.

Still unexplained for the three clines would be the occurr-
ence of their most specialized forms in or near the Guianas. Un-
known driving forces or not, one would not expect all three ex-
amples to become modified in the same general direction. If
there are extreme environmental conditions there now, they are
not apparent. The implication is that the relatively small size
of the Guiana pocket has promoted relatively rapid genetic change
there. The converse of this implication cannot be overlooked,
namely that while the Guiana pocket was small and promoting rapid
evolution (and may still be doing so), the rest of the ranges of
these species was (and is not) divided into similar small areas
of differentiation; or if it was, most signs of that differentia-
tion have disappeared, while the Guiana evidence remains. In the
first three examples of differentiation given above--the two
pairs of species, and M. oligantha--neither representative, in
the Guianas or inland, can clearly be said to be more specialized
than the other.

To sum up, it seems possible to explain all except one of
the six examples illustrating the Guiana relation largely on the
basis of present conditions but only with some strain; the expla-

nation of the exceptional case, M. oligantha, appears to require
moister conditions in the past and that of the others is eased by
theorizing both slightly drier conditions of the near past to in-
crease the isolation of the Guiana area and moister conditions at
some other time to reduce the gap between the Guiana region and
the moist area west of the intervening dry zone. Moister condi-
tions may have been related to an interglacial ocean embayment.
Doubtless habitat preferences and probably tolerance ranges are
factors in the distributions.

Therefore the evidence from the Memecyleae indicates only
one major center of differentiation in or immediately adjacent to
Amazonia, that of the northeastern Guianas and adjacent Amapá of
Brazil, with southeasterly extensions in the cases of two spe-
cies. Coincidence of the various distribution patterns of the
Memecyleae with the proposed refuges of central, southeastern,
southern, and western Amazonia sometimes occurs but cannot be
said to provide strong evidence for the existence of these cen-
ters. Speciation has been very active in Amazonia but does not
seem to have been closely associated with a few restricted geo-
graphic areas. Refuge boundaries may have been obscured by mi-
grations, of course. Distributions strongly support the well-
defined non-Amazonian coastal refuges of north Venezuela, Chocó,
and Serra do Mar, as well as the largely coastal northeast Guiana
center of the Memecyleae, all more or less isolated under present
conditions from other relatively moist forest areas of South
America. Of these the most sharply isolated, Serra do Mar, has
the most differentiation associated with it, followed by the
coastal Guianas. The Guiana center is not cut off so completely
from the Amazonian expanse as are the other coastal centers and
presumed refuges and consequently it has been possible for the
described relations to develop. Thus the tribal distribution
clearly reflects sharp differences in present conditions but not
lesser ones like the rainfall maxima of west and southwest Ama-
zonia (below).

A close association with high rainfall is shown in the Gui-
ana area. Here the present distributions of M. crassifolia, M.
dumetosa, the Guiana form of M. oligantha, the endemic M. franca-
villana, and the extreme forms of M. guianensis are mostly cen-
tered not in the proposed refuge area, which is inland, but near
the coast, where the rainfall is now greatest. There is no
assurance that this high rainfall once existed in the area of the
proposed refuge, although it may have, especially if the sea en-
croached to the area's edge.

This leads to another consideration, that of the present
rainfall maxima in Amazonia. As is well known, the precipitation
map of Reinke (1962) as adapted by both Haffer and Prance shows
only three definite maxima, one in eastern French Guiana and

adjacent Amapá, Brazil, one in eastern Ecuador, northeast Peru, and south Colombia, and one in the middle Madeira, Aripuanã, and Tapajós drainages. The first is close to the proposed Guiana re- fuge, the second is the Napo refuge of Haffer and Prance, and the third is the Madeira-Tapajós refuge of Haffer and the Rondonia-Aripuanã refuge of Prance. However, both Haffer and Prance show more than three refuges in Amazonia. Admittedly a detailed know- ledge of the rainfall is not to be had at present. Consideration of the fact that distribution in plants and animals is not merely historical but is controlled by present conditions leads to the old question of what the factors are that prevent spreading of organisms from their present ranges. Many factors can do so, but unless it can be shown that these are related to decreased rain- fall or some other drying influence in the surrounding region it does not necessarily follow that a localized inhabited zone is a probable prior area of residual forest in drier times. Centers of distribution and endemism can have other causes than amount of moisture.

In comparing centers of distribution the behavior of the particular organism is naturally of importance. Perhaps two kinds of animals, differentiated from a common ancestor follow- ing isolation yet retaining the same environmental needs, will on meeting again consciously exclude each other from their territor- ies and so maintain a clear line of separation. Plants, lacking such conscious exclusiveness, will move wherever the environment permits. Under the preceding circumstances two plant populations would in most cases be expected to intermingle, given enough time, permitting the occupation of more territory than in the case of the animals. Further, since one would not expect equal expansion in all directions from a refuge following climatic re- versal, the greater the territory occupied the less likely it is that the present center will coincide with that of the refuge.

Literature Cited   .

Haffer, J. 1969. Speciation in Amazonian forest birds. Science 165 (no. 3889, July): 131-137.

--------- 1974. Avian speciation in tropical South America. Pub. Nuttall Ornithological Club no. 14, Cambridge, Mass.

Morley, T. In press. Memecyleae of the New World. Flora Neotropica.

Müller, P. 1968. Die Herpetofauna der Insel von São Sebastião (Brasilien). Saarbrücker Zeitung, Saarbrücken.

Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. Acta Amazonica (Inst. Pesq. Amazonia, Manaus) 3 (no. 3): 5-26 (26 pp).

Reinke, R. 1962. Das Klima Amazoniens. Thesis, University of Tubingen.

Vanzolini, P. E. 1970. Zoologia sistemática, geografia e a origem das espécies. Univ. S. Paulo, Inst. Geogr., Ser. Monografias e Teses, 3.

Vanzolini, P. E. and Williams, E. E. 1970. South American anoles: the geographic differentiation and evolution of the Anolis chrysolepis species group (Sauria, Iguanidae). Arq. Zool. S. Paulo, 19: 1-240.
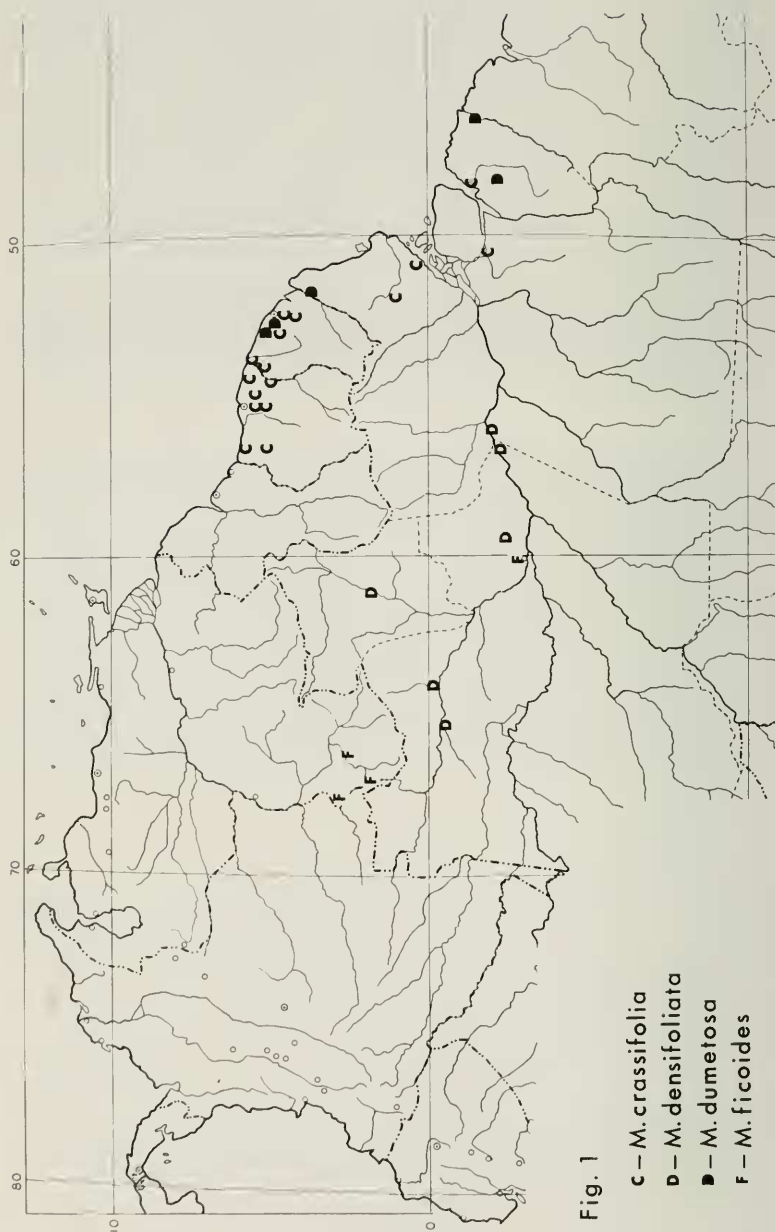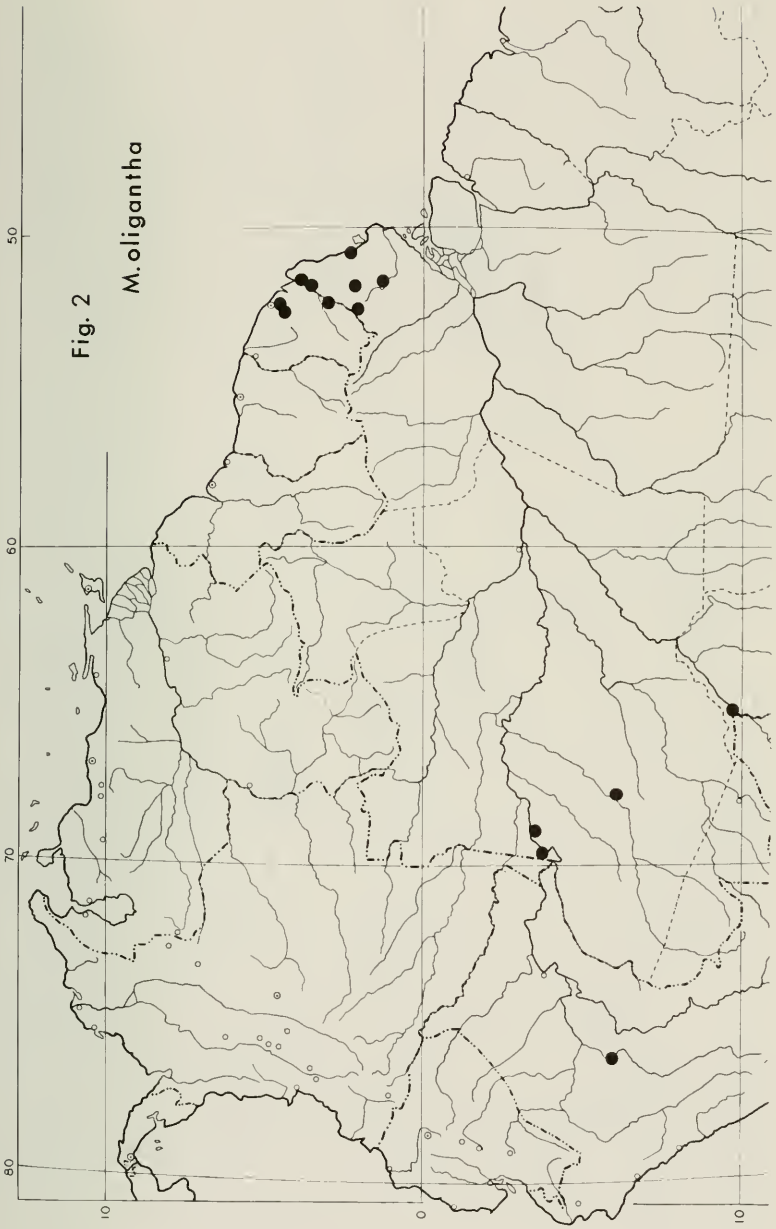
Fig. 1

c — M. crassifolia
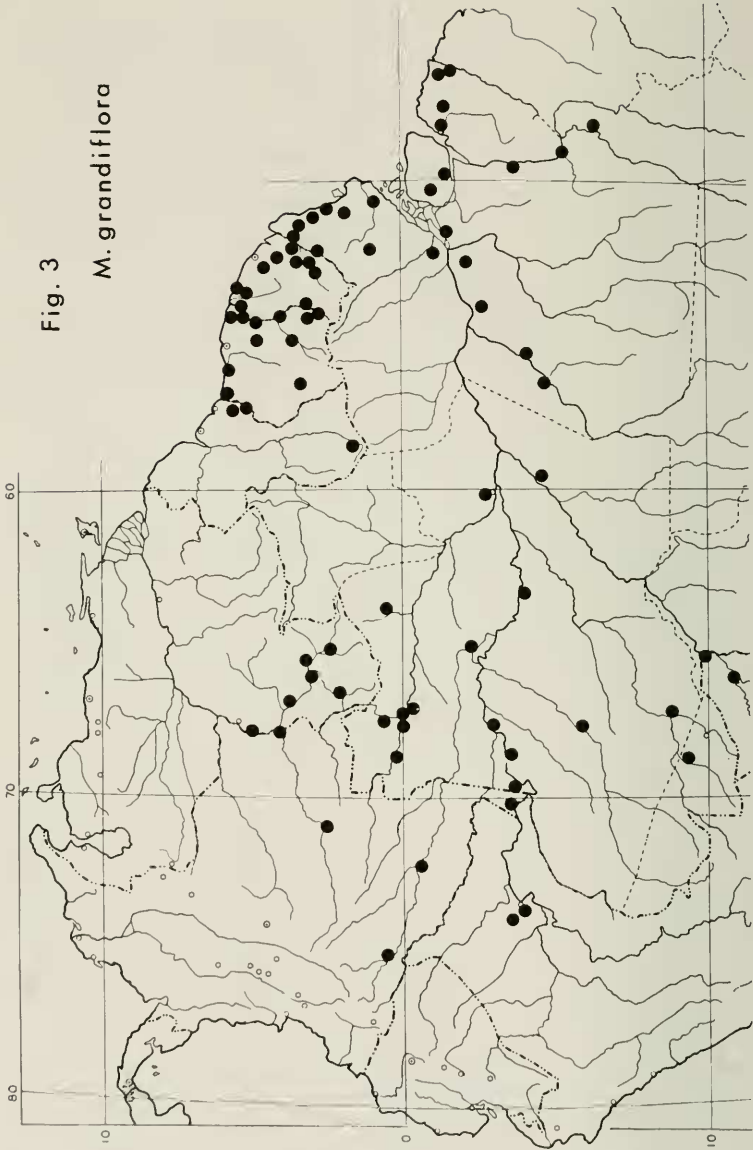D — M. densifoliata
■ — M. dumetosa
F — M. ficoides
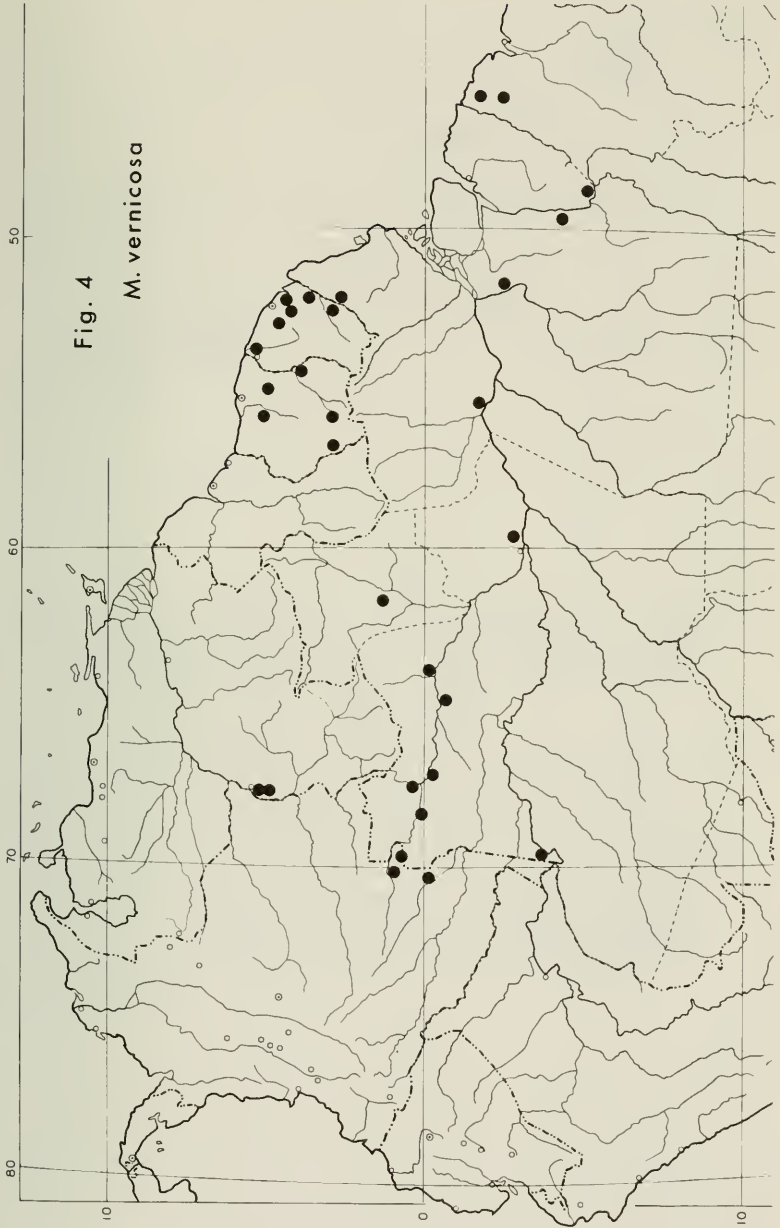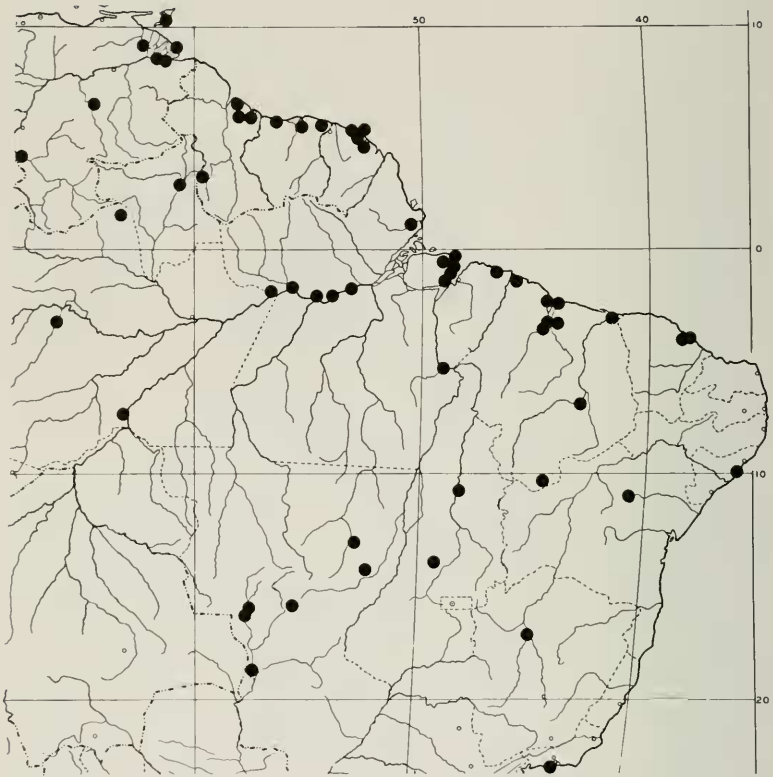
Fig. 2   M.oligantha

Fig. 3

M. grandiflora

Fig. 4

M. vernicosa

Fig. 5

M. guianensis